

# Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*

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The Northern Goshawk *Accipiter gentilis* typically prefers woodland habitat for nesting and hunting. In recent decades, however, the species has started colonising urban environments across Europe. Here I present the first study on the ranging behaviour of urban-breeding Goshawks. Each year from 1997 to 1999, I tracked a different adult male during the breeding season in the city of Hamburg, Germany (858 hours of total tracking time;  $n = 5364$  radio-fixes). All corresponding pairs raised young in the year of data collection (3, 3 and 4 juveniles). Average home range size was 863 ha (100% Minimum Convex Polygons). Males spent 88% of daylight hours in patches of urban green space (mainly parks) and made short but regular hunting excursions into the matrix of built-up habitat. Built-up habitat was used less frequently than expected from its percentage availability. However, 42% of all recorded kills ( $n = 143$ ) were made in this habitat type, indicating that it offered good foraging opportunities. Hawks spent 9.7% of daylight hours in active flight (1.8% inter-perch flights, 7.9% soaring). Daily activity patterns were bimodal, with peaks in the early morning and in the evening. I observed one hawk hunting regularly after sunset under artificial light conditions. Goshawks hunted by perched hunting (49%), soaring (33%), and fast contour-hugging flights (11%;  $n = 220$  hunts). Average hunting success was 16% ( $n = 176$  directly observed attacks), or one kill every 35 min of active flight. Home range size was smaller, time spent flying was shorter, and hunting success was higher for the monitored urban hawks than for non-urban individuals from earlier studies. Taken together, my data suggest that living conditions for Goshawks are more favourable in the city of Hamburg than in many non-urban environments.

Key words: *Accipiter gentilis*, behavioural plasticity, Northern Goshawk, predation ecology, radio-tracking, urban ecology and wildlife

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## INTRODUCTION

The Northern Goshawk *Accipiter gentilis* is generally considered a prime example of a shy forest raptor that is sensitive to human activity and depends on woodland habitat for nesting and hunting (e.g. Fischer 1995). In recent decades, however, the species has started colonising urban environments across Europe (Rutz *et al.* 2006). Goshawks currently occupy the full range of habitats found in modern, human-altered landscapes, including city centres (Cologne, Würfels 1999; Hamburg, Rutz 2001; Berlin, Altenkamp 2002).<sup>1</sup>

It is poorly understood why Goshawks started 'invading' urbanised habitats. It seems likely that a significant decrease in persecution levels facilitated behavioural adaptations, which ultimately enabled the species to nest in close proximity to humans, often far from its typical woodland habitat (Rutz *et al.* 2006). The phenomenon of urban-breeding in Goshawks is paralleled by similar trends in other *Accipiter* hawks (Eurasian Sparrowhawk *A. nisus*, McGrady 1991, Risch *et al.* 1996; Cooper's Hawk *A. cooperii*, Mannan & Boal 2000), and raptors in general (Andersen & Plumpton 2000, Love & Bird 2000).

In western Europe, Goshawks in wildland and exurban/rural habitats have been studied extensively (reviewed in Kenward 2006, Rutz *et al.* 2006). Much research, often using radio-telemetry, has focused on Goshawk ranging behaviour, providing detailed data on home range size (e.g. Kenward 1979, 1982, Ziesemer 1983, Kluth 1984, Straaß 1984), habitat use (e.g. Kluth 1984, Straaß 1984, Gamauf 1988, Löhmus 2001, Meier 2002), daily activity patterns (Kenward 1982), and hunting behaviour (Rudebeck 1950–51, Hantge 1980, Fox 1981, Kenward 1982). Similar information has been gathered for populations from northern Europe (reviewed in Kenward 1996, 2006, Torn-

berg *et al.* 2006), and for the North American subspecies *A. gentilis atricapillus* (reviewed in Kenward 2006, Rutz *et al.* 2006, Squires & Kennedy 2006).

The large body of literature on non-urban Goshawks contrasts with a striking lack of knowledge about their urban counterparts. Some studies on urban Goshawks have been conducted (reviewed in Rutz *et al.* 2006), but more work is needed to strengthen comparisons between populations in different habitats. Such comparisons promise valuable insights into the ultimate and proximate causes of population limitation (see Rutz *et al.* 2006), but also have potential relevance for Goshawk conservation. Cities may constitute 'ecological traps', i.e. habitats that are perceived by the birds as favourable (free nest sites, abundant food supplies, lack of inter- and intraspecific competition) but that are in reality unsuitable (elevated stress levels, reduced foraging efficiency, novel diseases, high collision risks; for an example, see Boal 1997).

In this paper, I present the first study on the ranging behaviour of urban-breeding Goshawks; dispersal movements of suburban- and urban-fledged Goshawks have been described before (Dietrich 1982, Rutz 2003b). My study had two main goals: (i) to contribute to a quantitative evaluation of the 'ecological trap hypothesis' by comparing the spatio-temporal organisation of urban-breeding Goshawks to that of non-urban individuals investigated in earlier studies; and (ii) to gather detailed observational data to inform more quantitative future work on urban-breeding Goshawks, especially studies in which radio-tagged hawks are monitored without visual contact. In my urban study area, conditions for observing Goshawks are excellent (hawks are highly stress tolerant; urban infrastructure facilitates close radio-monitoring), so I was able to collect data which

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<sup>1</sup>Marzluff *et al.* (2001) defined five main habitat types along the gradient of urbanisation. In order of increasing building density and proportion of built area (but not necessarily resident human density) they distinguish: wildland; exurban/rural; suburban; urban. Exurban and rural habitats differ in the type of matrix habitat (natural vs. agricultural). Goshawks live and have been studied in all of these habitats. In this paper, I will often collectively refer to Goshawks living in the first three habitats as 'non-urban' hawks, mainly because data come from a range of study habitats. To increase readability, I sometimes refer to 'woodland' habitat, by which I mean stretches of forest that can be situated either in wildland or exurban/rural landscapes.

are difficult, if not impossible, to obtain in such detail for Goshawks in wildland or exurban/rural habitats.

## METHODS

### Study area and subjects

This study was conducted in the city of Hamburg, Germany (53°34'N, 9°59'E). Each year from 1997 to 1999, I fitted the adult male of a different Goshawk breeding pair with a radio-transmitter, and subsequently tracked it throughout the breeding season. Nest sites of the pairs were located in an extensively used public park in the city centre (1997; hereafter referred to as 'pair 1' and its male as 'male 1'), on a hospital ground (1998; 'pair 2'), and on a large urban cemetery (1999; 'pair 3'), respectively. All three pairs successfully raised young in the year of data collection (Table 1). Further details on these pairs have been reported elsewhere (Rutz 2001, 2003a, b, 2004, 2005).

**Table 1.** Summary of radio-tracking information for three radio-tagged male Goshawks breeding in the city of Hamburg, Germany.

	Male 1	Male 2	Male 3
Basic information			
Year	1997	1998	1999
Trapping date	16.02	22.02	16.04
Age (years)	4	3	≥ 5
Juveniles	3	3	4
Tracking period	18.02 – 12.07	26.02 – 15.07	25.04 – 13.07
Tracking sessions	30	33	14
of which full days	21	16	6
Total tracking time (hours)	371	333	154
Number of radio-fixes <sup>a</sup>	2313	2111	940
of which standard fixes <sup>a</sup>	1980	1940	871
Number of subsampled fixes <sup>a</sup>	81	82	34

<sup>a</sup> 'Standard fixes' were recorded in 10-min intervals, and all remaining fixes were the result of opportunistic data collection. For statistical analyses, datasets were 'subsampled' to approximate temporal independence for consecutive radio-fixes.

I calculated the beginning of egg-laying from wing lengths of nestlings at the time of ringing (Kenward *et al.* 1993; tabulated values from Bijlsma 1997). Stages of the annual breeding cycle – pre-laying-, laying-, incubation-, nestling- and post-fledging-periods – were then computed, using literature values for egg-laying intervals (3 days), duration of incubation (38 days), and time of fledging (38 days after hatching) (Glutz von Blotzheim *et al.* 1971, Grünhagen & Görze 1995, Bijlsma 1997).

### Radio-tracking

Hawks were trapped near the nest with spring-net traps baited with live domestic pigeons (Karl bom 1981). They were equipped with 16-g tail-mounted radio-transmitters (Biotrack Ltd., Dorset, UK), using an adapted version of the method described by Kenward (1978) (tags were glued – but not sown – to the two central tail feathers). Tags had a built-in activity switch that altered the pulse rate of the radio-signal according to the birds' activity (Kenward 2001). By listening to the signal pattern, I was able to distinguish between *perching* (= slow pulse rate), *inter-perch flight* (= fast pulse rate), *soaring* (= fast pulse rate with regular modulation in amplitude), and *plucking* (= irregular bouts of slow and fast pulse rates), when birds were out of sight (see Kenward 2001). Direct observations confirmed that my scoring of activity types was reliable (see Rutz 2001).

Overall, birds were monitored about 1.5 times a week (Table 1). Continuous tracking was conducted from dawn to dusk on full-day sessions, and from dawn to midday, or from midday to dusk (in roughly equal proportions) on half-day sessions (Table 1). To sample the birds' behaviour under the full range of human activity levels, I distributed tracking sessions across the week, including weekends. I recorded radio-fixes with a portable Mariner Radar M-57 receiver (Mariner Radar Ltd., Suffolk, UK), a three-element hand-held Yagi antenna (Biotrack Ltd., Dorset, UK), and a mirror compass (Silva Ltd., Livingston, UK). Most of the time I used headphones to eliminate distracting traffic noise.

Compared with non-urban Goshawks, the individuals of my study were remarkably tolerant of human activity. It was possible to approach perched hawks as close as 20 m without disturbing them (Rutz 2003b, 2004). The 'tameness' of my study subjects and the excellent infrastructure of the urban environment enabled me to keep in close contact to the hawks, something that is difficult or impossible to achieve in non-urban settings (see Newton 1986). Most fixes were recorded by opportunistically homing-in on the tagged hawk (White & Garrott 1990); in fact, more than half of all 'standard fixes' (see below) were based on direct observations. All other locations were estimated by cross-triangulation (White & Garrott 1990, Kenward 2001) at a resolution of about 50–100 m (Rutz 2001). Most of the time, I followed hawks by bicycle, but in a few cases, when birds had travelled distances > 1.5 km, I searched for them using a car with a roof-mounted dipole antenna.

Fixes were recorded following two different sampling regimes: (i) *standard fixes* were recorded every 10 min (instantaneous sampling); and (ii) *extra fixes* were recorded between standard fixes whenever possible (continuous sampling). Additionally, every spatial movement of a bird, as indicated by the activity sensor of the radio-tag, was noted in a field notebook (for criterion, see below). All times were recorded as Central European Times (CET = GMT + 1 h), with summer time adjustment (GMT + 2 h) from end of March until the end of fieldwork in mid-July (Table 1). I decided to observe summer time in my analyses, because clock shifting changes human activity patterns which in turn may affect Goshawk ranging behaviour. In retrospect, however, it is clear from Figs 3 and 5 that ignoring summer time would not have changed any of the main conclusions (this was also confirmed quantitatively by analysing data separately for different time periods; for details, see Rutz 2001).

## Data analysis

### HOME RANGE SIZE AND HABITAT USE

To estimate home range sizes, I constructed Minimum Convex Polygons (MCPs; Kenward 2001).

This method was most suitable for the purpose of my study, because; (i) it is one of the most often used techniques and enables robust cross-study comparisons; (ii) it gives an intuitive approximation of the total area used by an animal; (iii) it makes no assumptions regarding the statistical independence of radio-fixes (e.g. De Solla *et al.* 1999), so whole datasets could be used. For all three hawks, visual inspection of incremental area plots (Kenward & Hodder 1996) suggested that home range sizes had stabilised towards the end of data collection (see Fig. 3.2 in Rutz 2001). All calculations were carried out with Ranges V-software (Anatrack Ltd., UK; Kenward & Hodder 1996).

I assessed habitat use by two different methods. *Qualitative description* – All standard fixes of a full-day tracking session were assigned to habitat categories given in Table 3. The number of fixes in a certain category was then used to estimate the percentage use of this habitat type for a given day. With this method it was possible to investigate how habitat use changed in the course of the breeding season. Additionally, means were calculated from values of individual tracking days to describe general habitat use. *Quantitative analysis* – Samples of standard fixes were sub-sampled with a random algorithm (picking 3 radio-fixes per full-day session, and 2 fixes per half-day session; for full details, see Rutz 2001, and for sample sizes, see Table 1), and locations were subsequently assigned to one of two habitat categories: *park* or *built-up habitat*. I then employed a standard use-availability design to test whether observed habitat use differed significantly from that expected from random movement (White & Garrott 1990).

I used GIS-software (ArcView GIS 3.2; ESRI 1996) to estimate the composition of habitat available to hawks at three different spatial scales (100% MCPs of individual hawks; sum of all three 100% MCPs; rectangular plot of 7200 ha, comprising all three 100% MCPs; water excluded in all cases). For each bird, habitat use and availability were then compared with  $\chi^2$ -goodness of fit tests with Yate's correction (Zar 1999).

#### ACTIVITY PATTERNS AND TIME BUDGETS

The number of movements per hour was used as a basic measure of locomotor activity. I defined a *movement* as a flight between two perches. When a bird was out of sight, a switch of the tag's activity sensor to fast pulse rate for at least 3 secs was interpreted as a spatial movement. I chose this criterion, because shorter bouts might have been caused by preening behaviour or balancing on a branch in windy weather conditions (C. Rutz, pers. observ.). I did not use any additional criteria, such as minimum spatial displacement or minimum perch time (note difference to Widén 1984, Newton 1986).

I distinguished between two activity types: *flight* and *non-flight* (= all activities without change of spatial position; e.g. perching, preening, plucking, feeding, and bathing). For flight-behaviour, I further distinguished between *inter-perch flights* and *soaring*. The distance travelled per full tracking day was estimated by connecting all standard fixes with straight lines and summing-up the lengths of all steps (Warkentin & Oliphant 1990). This distance was then used to estimate the time that a hawk had spent with inter-perch flights per day. The travelling speed of a Goshawk was set at  $15 \text{ m s}^{-1}$  ( $15.3 \text{ m s}^{-1}$ , Fox 1981;  $10\text{--}15 \text{ m s}^{-1}$ , Widén 1984). I computed the amount of time hawks spent soaring directly from my field notes (see above). The proportion of time spent with non-flight activities was then computed by subtracting the time spent flying (inter-perch flights and soaring combined) from the total tracking time.

For all standard fixes, the distance from the respective nest site was calculated using CAD-software (ArchiCAD 6.0; GEOvision, Frederikshavn, Denmark).

#### HUNTING BEHAVIOUR

I defined a *hunt* as either a direct attack on prey, or an active attempt by Goshawk to put itself into a position that was favourable for an attack on an individual prey or a group of prey visible to the observer (e.g. the attempt of a hawk to outfly a flock of pigeons). Repeated attacks on the same prey individual were counted as one hunt. Prey-

searching behaviour was *not* considered hunting in order to avoid misclassifications (note difference to Fox 1981).

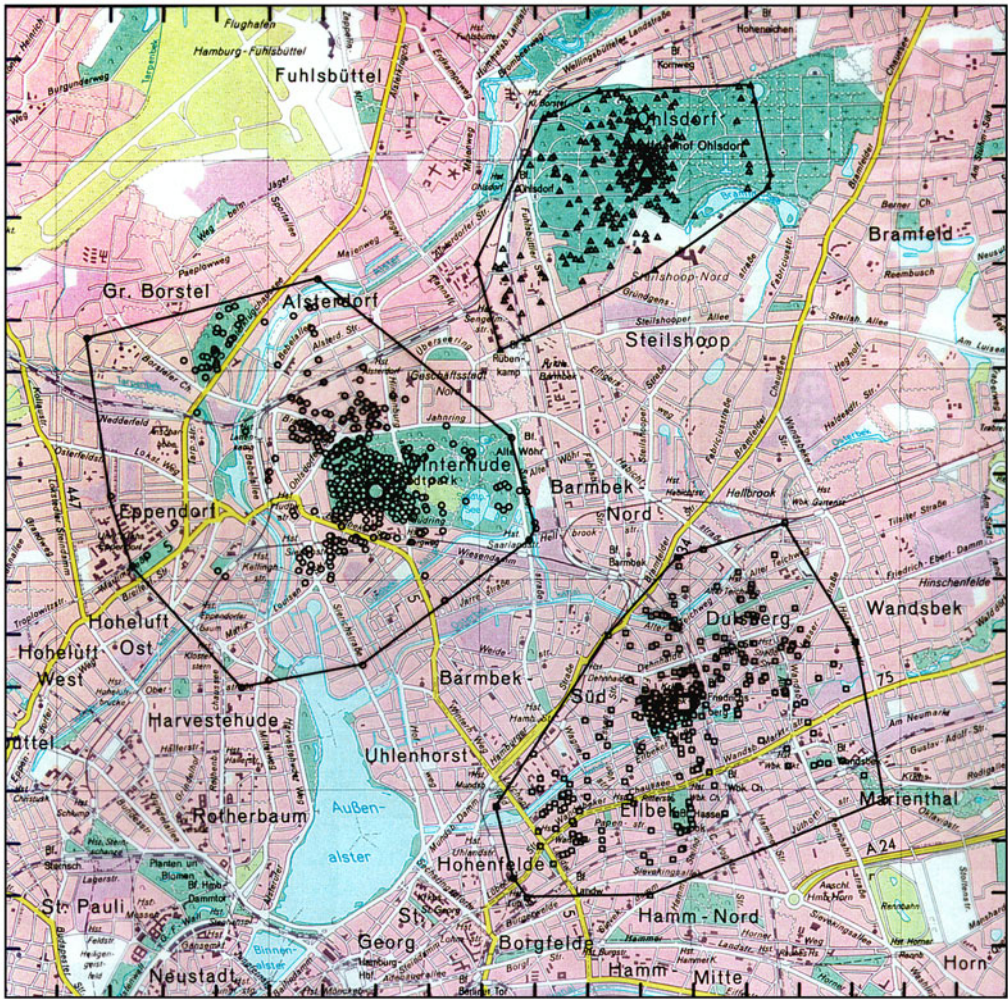
The following hunting techniques were distinguished (cf. Fox 1981). *Fast contour-hugging flight* – The hawk flew fast and low (at maximum 15 m above the ground) and used structures of the habitat for concealment (e.g. cars, houses, fences). Flushed prey was pursued in a tail-chase. *Perched hunting* – Prey was attacked by a hawk that was perched either in a tree or on an anthropogenic structure (e.g. antenna, house, or electricity pylon). If the hawk failed to kill a prey on the first strike and engaged in a pursuit, this hunting technique could not be distinguished from a tail-chase. Therefore, I only included unambiguous complete observations in the analysis. *Airborne hunting* – Hunts of this category were flown well above the canopy of forests and above houses. A soaring or gliding hawk attacked prey in a vertical stoop or a long-distance glide attack. Note that these hunts were not only launched at high-flying prey but also at individuals at or near the ground. *Other techniques* – This class includes all hunts that did not fall into any of the above categories, e.g. hunting by foot, nest-robbing, or hovering.

## RESULTS

### Home range size and habitat use

The total area visited by a Goshawk averaged 863 ha (100% MCP), but sizes differed substantially between individuals (Fig. 1, Table 2). After excluding locations farthest from the range centre, mean home range size was halved (421 ha, 95% MCP; Table 2). Home range size changed in the course of the breeding season, with the largest estimates for the post-fledging period in all three individuals. Ranges of males 1 and 2 appeared to contract from the pre-laying to the laying period (Table 2).

Goshawks spent 88% of daylight hours in park-like patches and made short but regular excursions into surrounding built-up habitat (Table 3A). The majority of standard fixes (85%) was recorded in the park where the nest site of a pair was located.



**Figure 1.** Home ranges (100% Minimum Convex Polygons) of three radio-tagged male Goshawks breeding in the city of Hamburg, Germany. Small symbols are standard radio-fixes recorded for the three hawks (pooled across all tracking sessions), and large symbols mark the nest sites of the corresponding breeding pairs. Tracking took place in different years, but all three individuals bred on their respective territories throughout the study period (1997–99), and there were no other known Goshawk territories in-between their nest sites. Tick marks are 500 m apart. Circles: male 1 (1997); squares: male 2 (1998); triangles: male 3 (1999).

Built-up habitat was used less frequently than expected from random habitat use, irrespective of how habitat availability was estimated (Table 3B). The 100% MCP of male 3 was dominated by park-like structures (66%), whereas the home ranges of the other two hawks had higher contributions of

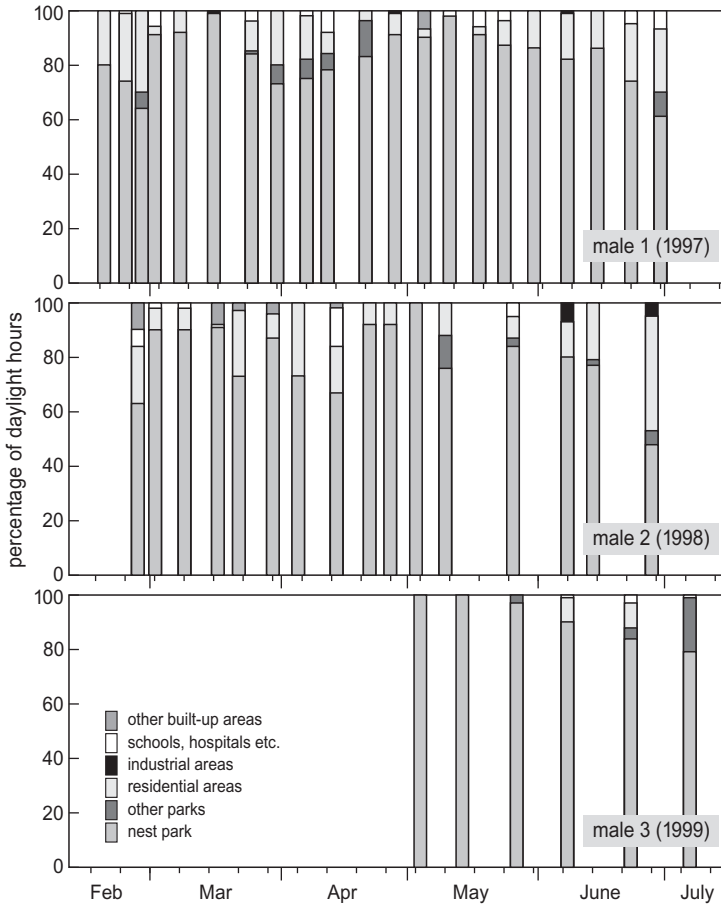
built-up habitat (26% park, male 1; 13%, male 2). Habitat use changed in the course of the breeding cycle (Fig. 2): daily use of built-up habitat seemed to oscillate with three maxima (end of February, end of March, end of June) and two minima (mid-March, early to mid-May).

**Table 2.** Home range sizes (in ha) of urban-breeding male Goshawks. Minimum Convex Polygons (MCP) were constructed for datasets collected by continuous radio-monitoring (number of radio-fixes in brackets). (A) Data pooled across the breeding season, and (B) data analysed separately for five different stages of the breeding cycle. For methodological details, see text.

		Male 1	Male 2	Male 3	Mean
A					
MCP (100%)	Pooled	1189 (2313)	921 (2111)	480 (940)	863
MCP (95%)	Pooled	342 (2197)	568 (2005)	354 (893)	421
B					
MCP (100%)	Pre-laying	544 (371)	478 (538)	–	511
	Laying	374 (69)	389 (166)	–	382
	Incubation	551 (441)	157 (464)	–	354
	Nestling	324 (872)	641 (659)	244 (469)	403
	Post-fledging	976 (560)	681 (284)	475 (471)	711

**Table 3.** Habitat use of urban-breeding male Goshawks. (A) Radio-fixes collected during full-day tracking sessions (cf. Fig. 2) were assigned to one of six habitat categories; daily values were then used to compute average use (sample sizes: 21 full-day tracking sessions, male 1; 16 sessions, male 2; 6 sessions, male 3). (B) Fixes of sub-sampled datasets (cf. Table 1) were assigned to one of two habitat classes; observed habitat use was then compared to expected habitat use (assuming random movements). The composition of habitat available to hawks was computed at three different scales: (i) within the 100% MCPs of individual males (first value); (ii) for the combined 100% MCPs of all three hawks (second value); and (iii) for a rectangular plot of 7200 ha, comprising all three 100% MCPs (third value). *P*-values refer to all three tests calculated per hawk. For methodological details, see text.

Habitat class		Male 1	Male 2	Male 3	Mean
A					
Park	Nest park (%)	83	80	92	85
	Other parks (%)	2	1	5	3
	Sum (%)	85	82	96	88
Built-up	Residential (%)	12	14	3	10
	Industrial (%)	0	1	0	0
	School/hospital (%)	2	2	1	2
	Other (%)	0	2	0	1
	Sum (%)	15	18	4	12
B					
Park	Available (%)	26, 29, 24	13, 29, 24	66, 29, 24	–
	Used (%)	88	82	91	–
Built-up	Available (%)	74, 71, 76	87, 71, 76	34, 71, 76	–
	Used (%)	12	18	9	–
	<i>P</i> -values	< 0.0001	< 0.0001	< 0.005	–



**Figure 2.** Habitat use of urban-breeding male Goshawks. All standard radio-fixes were assigned to one of six habitat classes. Data are only shown for full-day tracking sessions, when hawks were monitored without interruption from dawn to dusk. Minor tick marks on the x-axes indicate Mondays. For further details, see text and Table 3.

There was no indication that the birds' stress tolerance (see Methods) varied with habitat type (e.g. park vs. built-up), but male 2 showed some interesting behavioural changes after sunset (see below).

### Activity patterns and time budgets

Hawks spent 9.7% of daylight hours in active flight (Table 4A). On average, they made 4.3 inter-perch flights and travelled a distance of about 1 km per hour (Table 4B). Daily activity patterns were bimodal, with peaks in the early morning and in the evening (Fig. 3A). This pattern was still present, although less clear, when data were plotted separately for the time before and after hatching

of young; see Fig. 5.1 in Rutz (2001). In male 1, average daily activity was higher after hatching than in the time before (Fig. 4A). No such difference was found in the other two individuals, or for the pooled datasets. In males 1 and 2, time spent with thermal soaring was distributed evenly across the day with a minor peak around midday (Fig. 3B). Male 3 soared more per day than the other two individuals (Table 4B), and exhibited two marked activity peaks separated by a resting period around midday (Fig. 3B).

Hawks were on average 343 m away from the nest (Table 4B), with a maximum recorded distance of 3090 m for male 1 (cf. Fig. 1). Distance from the nest site, with data pooled across the

**Table 4.** (A) Time budgets for daylight hours (mean, range), (B) movement characteristics (mean  $\pm$  1 SD), and (C) hunting statistics (where appropriate: mean  $\pm$  1 SD) for urban-breeding male Goshawks. Sample sizes are given in brackets. Hunting success was calculated for all hunts that were witnessed (i.e. excluding inferred cases; cf. Table 5). For methodological details, see text.

	Male 1	Male 2	Male 3	Mean
<b>A</b>				
Inter-perch (%) <sup>a</sup>	1.7, 0.5–2.7	1.7, 0.3–3.1	2.1, 1.4–3.5	1.8
Soaring (%) <sup>a</sup>	3.8, 0.0–15.9	4.0, 0.0–12.5	16.0, 9.0–25.8	7.9
Non-flight (%) <sup>a</sup>	94.5, 81.6–99.5	94.4, 85.6–99.7	82.0, 70.7–89.5	90.3
<b>B</b>				
Number of movements per hour <sup>b</sup>	5.0 $\pm$ 3.3 (282)	4.1 $\pm$ 3.7 (288)	3.8 $\pm$ 3.4 (142)	4.3
Soaring per hour (min) <sup>b</sup>	2.3 $\pm$ 6.9 (283)	2.3 $\pm$ 6.3 (287)	9.7 $\pm$ 14.3 (84)	4.8
Travelled distance per day (m) <sup>a</sup>	13460 $\pm$ 5750	13020 $\pm$ 6160	19180 $\pm$ 9340	15220
Distance (m) per hour <sup>a</sup>	920 $\pm$ 350	910 $\pm$ 430	1120 $\pm$ 510	983
Distance from nest (m) <sup>a</sup>	300 $\pm$ 430	340 $\pm$ 470	390 $\pm$ 450	343
<b>C</b>				
Hunting success (%) <sup>c</sup>	13 (13, 100)	17 (9, 53)	17 (4, 23)	16
Total number of kills	72	47	26	–
Total estimated hunting time (min)	1226	1139	1667	–
Estimated kill rate	1 per 17 min	1 per 24 min	1 per 64 min	1 per 35 min
Prey weight (g) <sup>d</sup>	185 $\pm$ 109 (64)	297 $\pm$ 229 (34)	215 $\pm$ 112 (16)	232
Distance of kill from nest (m) <sup>d</sup>	619 $\pm$ 590 (68)	643 $\pm$ 499 (46)	744 $\pm$ 380 (24)	669
Time spent at kill site (min) <sup>d</sup>	19 $\pm$ 21 (51)	57 $\pm$ 72 (44)	34 $\pm$ 36 (23)	37

<sup>a</sup> Sample sizes: 21 full-day tracking sessions, male 1; 16 sessions, male 2; 6 sessions, male 3.

<sup>b</sup> Sample sizes in brackets are the number of 1-hour bouts.

<sup>c</sup> Sample sizes in brackets are: kills (first value), and the total number of directly observed attacks (second value).

<sup>d</sup> Sample sizes in brackets are the number of prey items.

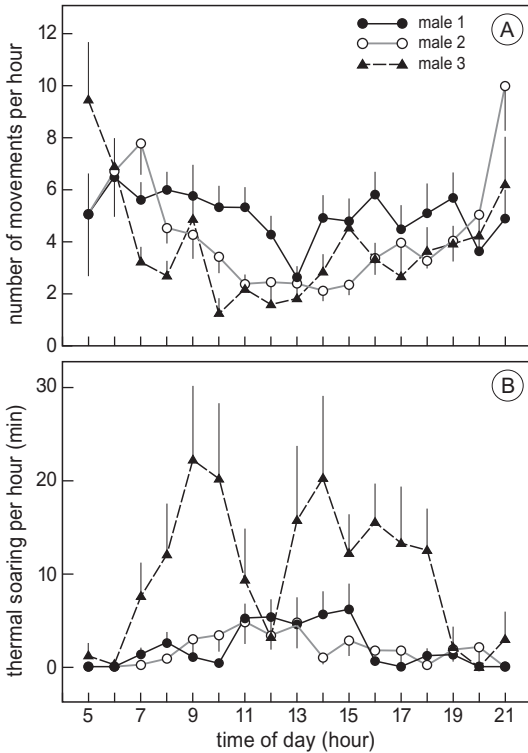
entire breeding season, did not show systematic diurnal patterns, but in male 2 there was a tendency to stay further away from the nest during mornings and evenings (Fig. 5). Plotting data separately for the different phases of the breeding cycle did not reveal any consistent patterns; see Fig. 5.4 in Rutz (2001).

### Hunting behaviour

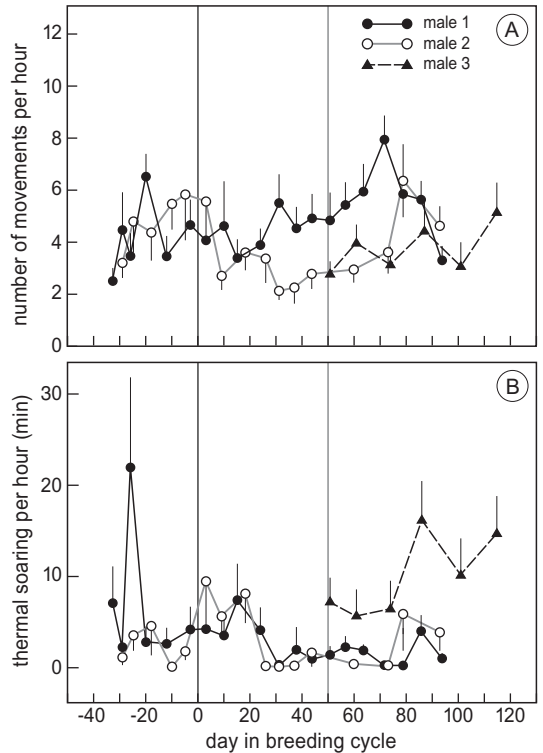
Average hunting success was 16% ( $n = 176$  directly observed attacks; Table 4C). Under the conservative assumption that hawks were exclusively hunting during periods of active flight (9.7% of daylight hours), this translates into an average success rate of one kill per 35 min of hunting

(Table 4C). All tagged hawks showed increased locomotor activity prior to a successful kill, and reduced activity thereafter (Fig. 6).

Kills were distributed evenly across daytimes (data not shown; see Fig. 6.5 in Rutz 2001). For both males with sufficient data (males 1 and 2), the number of kills per day increased throughout the breeding season (data not shown; see Fig. 6.4 in Rutz 2001). Mean prey weight was 232 g ( $n = 114$ ), the mean distance between kill site and nest was 669 m ( $n = 138$ ), and hawks spent on average 37 min ( $n = 118$ ) at a kill site (Table 4C). On average, 42% of a male's kills were recorded in built-up habitat (48%, when kills were pooled across birds;  $n = 143$ ); about 77% (78%, pooled)



**Figure 3.** Daily activity patterns of urban-breeding male Goshawks. (A) Number of movements per hour, and (B) time spent soaring per hour. Tick marks on the x-axes indicate the beginning of 1-hour bins. Values are shown as means with one SE.

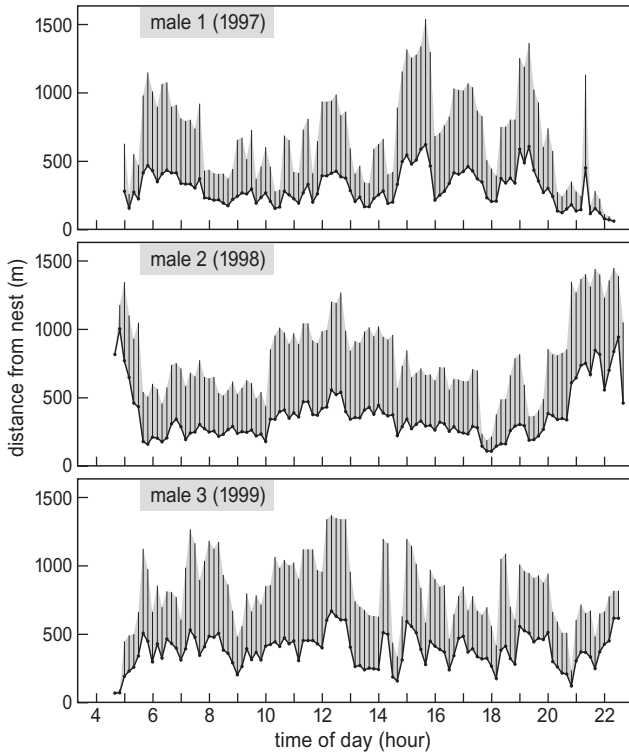


**Figure 4.** Flight activity of urban-breeding male Goshawks in the course of the breeding cycle. (A) Number of movements per hour, and (B) time spent soaring per hour. Day '0' is the day on which the first egg of a clutch was laid (black vertical line), and on day '50', all three pairs had the first hatchling (grey vertical line). Daily values are shown as means with one SE.

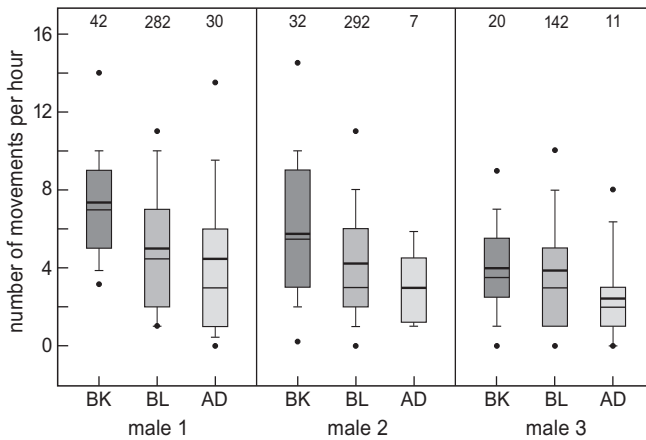
of all kills in built-up habitat were made in residential areas, 55% (57%, pooled) of which occurred in backyards. The distribution of all attacks (kills and unsuccessful attempts combined) across habitat types is given in Table 5B.

Hawks hunted by perched hunting (49%), soaring (33%), and fast contour-hugging flight (11%;  $n = 220$ ), with some notable individual differences (Table 5A). Male 1 was the only bird that used anthropogenic structures for perched hunting at daytimes. It regularly used the roof-top of the 'Planetarium' (300 m from the nest; see Fig. 1 in Rutz 2004) for perching, and launched a total of 21 attacks from this vantage point (2 of which

successful). Males 1 and 2 were often foraging in residential areas (Table 3A), flying along below the roof-line of housing blocks and flipping abruptly over roofs to dive at Feral Pigeons *Columba livia*, Magpies *Pica pica* and Blackbirds *Turdus merula* in backyards (so-called 'backyard jumping'; see Figs 2 and 6 in Rutz 2004). On other occasions, they used parked cars, fences and other objects for concealment during low quartering flights (contour-hugging). All three males were observed stooping at pigeon flocks and individual prey (sometimes prey were at ground-level in residential areas). Male 3 had a comparatively high proportion of airborne hunts (Table 5A), associated with its preference for



**Figure 5.** Distance from the nest for urban-breeding male Goshawks. For each hawk, data were pooled across tracking sessions (full- and half-day sessions combined). Tick marks on the x-axes indicate the beginning of 1-hour bins. Values are shown as means plus one SD.



**Figure 6.** Relationship between locomotor activity (number of movements per hour) and hunting behaviour in urban-breeding male Goshawks. The radio-tagged hawks seemed to be more active one hour before a kill (before kill, BK) than usual (baseline, BL; all values pooled). Conversely, in the hour after having delivered prey to the nest site (after delivery, AD), activity levels seemed to be reduced. Box plots show: 25th and 75th percentile (box), 10th and 90th percentile (whiskers), 5th and 95th percentile (circles), as well as median (thin line) and mean (bold line). Numbers indicate sample sizes.

**Table 5.** Hunting behaviour of urban-breeding male Goshawks. (A) Use of different hunting techniques, and (B) distribution of hunts across habitat types (both as percentage of the number of hunts). Kills and unsuccessful attacks are pooled. Percentage values in (A) are based on hunts for which the hunting technique could be determined, and values in (B) are based on all hunts (for male 2, habitat type was only known in 89 cases). Deviations from 100% are due to rounding. For methodological details, see text.

	Male 1	Male 2	Male 3	Mean
Number of hunts <sup>a</sup>	159 (132)	91 (59)	45 (29)	–
<b>A</b>				
Fast contour-hugging	11	15	7	11
Perched hunting	69	58	21	49
Airborne hunts	11	19	69	33
Other techniques	10	8	3	7
<b>B</b>				
Park				
Nest park	58	47	84	63
Other parks	2	1	9	4
Built-up				
Residential	28	49	4	27
Industrial	3	0	0	1
School/hospital	7	1	0	3
Other	2	1	2	2

<sup>a</sup> Sample sizes in brackets are the number of hunts for which the hunting technique could be determined.

prolonged thermal soaring bouts (see above; Figs 3B and 4B). Other hunting techniques included (pooled): hunting on foot (1 unsuccessful attempt; Rabbit *Oryctolagus cuniculus*), nest-robbing (15 attempts, 11 of which successful; 10× Magpie, 4× Jay *Garrulus glandarius*, 1× Carrion Crow *Corvus corone*), and hovering (1 unsuccessful attempt; Blackbird).

On twelve occasions, male 2 was observed ranging after sunset under artificial light conditions (three unsuccessful hunts, and four kills). On 2 March (at 18:13), this male attacked Feral Pigeons at their roost site on a roof-top, and on

two other occasions it engaged in tail-chase hunts with individual Feral Pigeons in residential areas (26 May, 21:54; 12 June, 22:23). Around sunset, this hawk showed striking behavioural changes: when 'patrolling' residential areas, it would routinely perch on anthropogenic structures (12 June, balcony; 12 and 28 June, chimney; 12 and 25 June, roof-top). Such behaviour was never observed in this bird during daytime, despite its overall stress tolerance (see above).

## DISCUSSION

### Home range size

Maximum home range size (100% MCP) for the three urban-breeding male Goshawks in Hamburg was c. 1000 ha. This agrees well with Würfels' (1994) estimate for Goshawks breeding in the city of Cologne, which was based on the spacing of nesting territories and the distribution of the hawks' presumed hunting habitat. It is worth noting that, for the Hamburg birds, Kernel home range estimators produced values which were about an order of magnitude smaller than the MCP values (Kernel estimators take into account the intensity with which certain areas within the range are used; see Table 3.2 in Rutz 2001).

Non-urban Goshawks have much larger home ranges (reviewed in Kenward 2006, Squires & Kennedy 2006); based on the collection of individually identifiable moulted feathers, Brüll (1953) estimated 3000–5000 ha for pairs at the rural periphery of Hamburg, and Ziesemer (1983) reported 1500–5000 ha for radio-tagged hawks in nearby parts of Schleswig-Holstein. Winter and non-breeder ranges are even larger (Kenward 1996, 2006, Ziesemer 1999). Likewise, urban-breeding Cooper's Hawks and Red-shouldered Buzzards *Buteo lineatus* have smaller home ranges than their non-urban counterparts (Bloom & McCrary 1996, Mannan & Boal 2000), but no such difference was found in other raptor species (e.g. Sparrowhawk, McGrady 1991; Merlin *Falco columbarius*, Sodhi & Oliphant 1992). The home range sizes I recorded for urban Goshawks are similar to

those reported for smaller bird-eating raptors in urban environments (e.g. 403 ha, Sparrowhawk, McGrady 1991; 820 ha, Merlin, Sodhi & Oliphant 1992).

Earlier studies have demonstrated that, in many raptor species, home range size varies as a decreasing function of food availability (reviewed in Newton 1979; examples in Marquiss & Newton 1981, Kenward 1982, Ziesemer 1983, Kenward & Widén 1989, Selås & Rafoss 1999). On this evidence, small home ranges observed in urban Goshawks and other urban-breeding raptor species suggest that foraging opportunities in cities are better than those in (most) non-urban settings. This interpretation is supported by a suite of other findings, as I will describe later. Future studies would ideally estimate home range sizes along an urban-rural habitat gradient, together with measures of food availability and Goshawk diet choice.

Home ranges of the three neighbouring hawks did not overlap (see Fig. 1). Tracking took place in different years, but the same individuals bred on their respective territories during 1997–99 (birds were identified by comparing moulted feathers, following Bijlsma 1997; no feathers available for male 2 in 1999), presumably using similar hunting ranges over the years (cf. Sodhi & Oliphant 1992). Little is known about the spacing of Goshawk home ranges during the breeding season (reviewed in Kenward 2006), but substantial overlap has been reported for some non-urban habitats (Ziesemer 1983, Squires & Kennedy 2006). The wide spacing observed in the city of Hamburg has recently been confirmed with a larger sample of radio-tagged hawks (C. Rutz *et al.*, unpubl. data), and it probably results from the unusual distribution of resources in this urban landscape. Suitable nest sites (parks) have a patchy distribution and are far apart in relation to the overall high abundance of prey in built-up areas (for further discussion, see Rutz *et al.* 2006). It is interesting to note that, on several occasions, I observed (unmarked) Goshawks at the nest sites of males 1 and 2 (Rutz 2005), confirming that the hunting ranges of these territory holders were visited by non-breeding hawks.

### Habitat use

In many large cities, patches of green space are interspersed in a matrix of built-up habitat, forming a mosaic-like pattern (see Fig. 1). All three Goshawks used the urban habitat in a non-random fashion. Each hawk spent most of the time in the park where its nest was located, but made regular excursions into the surrounding built-up habitat. I have not formally investigated whether hawks selected park-edges, but I suspect that urban Goshawks depend much less on hunting near habitat-edge zones than their rural counterparts (Kenward 1982, 2006). I have provided photos of typical hunting habitat elsewhere (see Rutz 2004).

It should not be concluded from my data that birds *preferred* parks and *avoided* built-up habitat. A large proportion of radio-fixes in parks were simply due to the males' association with their territories and families: Goshawk males share many parental duties (e.g. nest-building and brooding; Kenward 2006), they closely guard their mates before and during egg-laying ('mate attendance' is a paternity assurance strategy; data for males 1–3 are given in Rutz 2005), and they often rest in the nest area after delivering prey (see Fig. 6). Perhaps more importantly, about half of all kills were made during short visits to residential areas, indicating that this habitat was of considerable importance for foraging. I decided against discarding fixes within the inner nesting area prior to analysis, because my observations showed that all three hawks hunted regularly in the vicinity of their nests (Rutz 2001, 2004).

Hunting by Goshawks in residential areas has been observed in other cities, such as Saarbrücken (Dietrich 1982), Cologne (Würfels 1994), and Berlin (Altenkamp 2002). Many other raptor species hunt in highly-urbanised habitats, including Eurasian Sparrowhawk (Frimer 1989, McGrady 1991, Grünhagen 1993, de Baeremaeker 2004), Cooper's Hawk (Murphy *et al.* 1988, Mannan & Boal 2000), Peregrine Falcon *Falco peregrinus* (Cade & Burnham 2003), Common Kestrel *F. tinnunculus* (Piattella *et al.* 1999, Kübler *et al.* 2005), Common Buzzard *Buteo buteo* (C. Rutz, pers. observ.), and Honey Buzzard *Pernis apivorus* (C. Rutz, pers.

observ.). Merlins in Saskatoon hunt in built-up areas in the city centre, but they also undertake foraging trips into the surrounding open landscape (Warkentin & Oliphant 1990, Sodhi *et al.* 1991, Sodhi & Oliphant 1992). Interestingly, some urban-breeding raptor species – or at least some individuals of a given population – seem to avoid built-up areas (Murphy *et al.* 1988, England *et al.* 1995, Bloom & McCrary 1996, Seijas 1996).

### Activity patterns and time budgets

Hawks spent about 10% of daylight hours in active flight, of which roughly one-fifth were attributable to inter-perch flights and the rest to thermal soaring. Daily flight activity of three male breeders in New Mexico, USA, was almost double my estimate (18.2%, Kennedy 1991), but data collection was restricted to the nestling- and post-fledging periods. However, as I could not find any evidence that flight activity in my urban birds increased in the course of the breeding cycle (see Fig. 5.3 in Rutz 2001), I consider the results of the two studies comparable. Four wintering male Goshawks in Sweden spent about 7.1% in active flight (Widén 1984), which is close to the Hamburg value. Comparing summer and winter data is problematic because it is difficult to predict the relative effects of food demands and prey availability on Goshawk activity patterns. During the breeding season, male hawks may be expected to show elevated activity levels because they have to provide food for their families; this idea is indeed supported by my observation that hunting behaviour was associated with increased locomotor activity (see also Rijnsdorp *et al.* 1981, Widén 1981, Warkentin & Oliphant 1990). On the other hand, the availability of abundant and vulnerable juvenile prey in summer may increase the hawks' general foraging efficiency. Nevertheless, Kennedy's (1991) data suggest that urban Goshawks spend less time in active flight than non-urban individuals.

The urban Goshawks flew less often (every 14 min) than non-urban hawks (every 4 min, Kenward 1982; every 9 min, Widén 1984) but travelled greater distances (15 km day<sup>-1</sup>, this study; 6 km day<sup>-1</sup>, Kenward 1982). This difference was

probably mainly due to the comparatively higher proportion of soaring in my urban birds, when they travelled much larger distances than the inter-perch distances of 100–200 m estimated by Kenward (1982). Neither Kennedy (1991) nor Widén (1981) were able to distinguish between inter-perch flights and thermal soaring. Widén (1981), however, concluded that most recorded flights in his dataset were probably short flights between perches. This would imply that the urban hawks spent a comparatively larger amount of time soaring than non-urban birds. Soaring in urban Goshawks could be associated with biotic (vulnerability of urban prey to stooping attacks), or abiotic factors (better thermal upwinds in cities; collision risk during low quartering flights), or both. In this context, it is worth noting that stooping was an important hunting technique in my urban hawks (see below).

The bimodal daily activity pattern suggests that hawks had two main hunting phases per day, separated by a resting period around midday (although note that hunting success was evenly distributed across daytimes). Urban Goshawks seem to be able to obtain a sufficient amount of food within just two periods of peak activity, probably because of high prey abundance and excellent kill rates (see below). Some studies reported bimodal prey-delivery rates at non-urban Goshawk nests (reviewed in Kenward 2006, Squires & Kennedy 2006), but deliveries do not necessarily reflect activity patterns of provisioning males (Rutz 2001). The only study, to my knowledge, to explore diurnal movement patterns for radio-tagged non-urban Goshawks found fairly high levels of flight activity throughout the day (Widén 1984), suggesting that hawks had to keep hunting to meet their daily energy requirements. However, data were collected during the winter, and are – for reasons discussed in detail above – not directly comparable to my results. More detailed radio-tracking studies are needed to establish whether bimodal activity patterns are unique to urban Goshawks.

### Hunting behaviour

Hunting success of the three urban males (16%)

was considerably higher than that of non-urban individuals (5.3%,  $n = 152$  chance observations, Hantge 1980; 6%,  $n = 79$  observations during radio-monitoring sessions, Kenward 1982). This difference between habitats was even more pronounced, when foraging success was expressed as a kill rate: one kill per 35 min of active flight (hunting) in urban Hamburg compared to one kill per 262 min in hawks hunting in countryside habitat in South England (Kenward 1982).

Urban Goshawks spent only 12% of daylight hours in built-up habitat, but they made 42% of all their kills in this habitat type, suggesting that it offered excellent hunting opportunities. This observation is consistent with data on the hunting behaviour of other urban-breeding raptor species (for references, see above). Some urban-breeding species, however, have been reported to fly large distances to reach good foraging grounds (e.g. England *et al.* 1995, Seijas 1996).

The tagged birds used all three main hunting techniques of non-urban Goshawks, namely fast contour-hugging flight, perched hunting, and airborne hunting (Glutz von Blotzheim *et al.* 1971, Fox 1981, Fischer 1995, Kenward 2006). However, I observed some interesting variants of these basic techniques, which are striking examples of how this forest raptor can adapt to novel environments (for further discussion, references and photos, see Rutz 2003b, 2004, Rutz *et al.* 2006). Most notable are: (i) Peregrine-like perched hunts from exposed vantage points like roof-tops and TV aerials; (ii) 'backyard jumping' and low quartering flights in residential areas where buildings and other objects are used for cover during surprise attacks; and (iii) foraging after sunset under artificial light conditions (see also Dietrich 1982). It is worth noting that (aspects of) these three techniques were also observed in two urban-fledged, radio-tagged hawks (offspring of male 1 in 1997) on their post-fledging dispersal in metropolitan Hamburg (Rutz 2003b). I will investigate elsewhere whether hunting behaviour and attack success of urban Goshawks vary with habitat type and/or prey species (C. Rutz & R. Kenward, in prep.).

### Concluding remarks

Home range size was smaller, flight activity was lower and hunting success was higher for the monitored urban hawks than for non-urban individuals from other studies. Taken together, my results suggest that living conditions for Goshawks in Hamburg are more favourable than those in typical non-urban environments. Other pieces of circumstantial evidence corroborate my radio-tracking results: breeding densities and fecundity rates observed in Goshawk populations in Hamburg (C. Rutz, unpubl. data), Berlin (Altenkamp 2002), and Cologne (Würfels 1994, 1999) exceed those in nearby rural areas (Rutz *et al.* 2006), and adult and juvenile mortality rates in urban hawks seem low (C. Rutz, unpubl. data). We need more data on Goshawk ranging behaviour and population demography from other cities to confirm and generalise these tentative conclusions.

The question remains why cities have only recently been colonised by Goshawks. Comparing colonised and uncolonised cities can shed light on the ultimate reasons of invasions (see Rutz *et al.* 2006), and the proximate mechanisms of city-colonisations may be accessible to experimentation, involving the controlled release of Goshawks into uncolonised cities. In any case, every opportunity should be used to study urban Goshawks where they exist. Perhaps more importantly, any new colonisation event should be monitored in detail from the early stages, when first pioneer pairs settle.

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## SAMENVATTING

Het beeld van de Havik *Accipiter gentilis* als schuwe bos-bewonende roofvogel is de laatste decennia in grote delen van Europa drastisch op zijn kop gezet. Tegenwoordig bewoont deze toppredator elk denkbaar habitat zolang er bomen staan, inclusief het industrieel-agrarische complex en de centra van steden. Hoe dit zo kon gebeuren, is verre van duidelijk. Misschien dat de afzwakkende vervolging de soort minder schuw heeft gemaakt, en er uiteindelijk toe heeft geleid dat zelfs steden werden gekoloniseerd. Een trend overigens die bij veel roofvogelsoorten is vastgesteld.

Dit onderzoek in Hamburg beschrijft in detail het leven van mannelijke stadshaviken tijdens de broedtijd. Hiertoe werd in drie opeenvolgende jaren telkens een ander mannetje van een zender voorzien en op de voet gevolgd. Hun activiteitsgebieden varieerden in omvang van 480 tot 1189 ha (gemiddeld 863 ha, exclusief uitbij-

ters 421 ha). Bij alle mannetjes was het activiteitsgebied het grootst na het uitvliegen van de jongen. De Haviken zaten 88% van de daglichtperiode in parkachtige stads-enclaves, van waaruit ze korte maar frequente uitstapjes naar de omringende bebouwing maakten. Stadsbebouwing werd minder vaak bezocht dan op grond van een willekeurige habitatkeus verwacht kon worden. De Haviken besteedden 9,7% van de daglichtperiode aan vliegen. Per uur legden ze gemiddeld een afstand van 1 km af, hoppend van plek naar plek (4,3 vluchten/uur). Activiteitspieken vielen in de vroege ochtend en in de avond. Gemiddeld zaten de mannetjes op 343 m van het nest, met als uitschieter 3090 m. Van 176 rechtstreeks geobserveerde vangpogingen was 13–17% (gemiddeld 16%) succesvol, wat neerkomt op één vangst per 35 minuten actief jagen. De vangsten waren gelijkelijk over de dag verdeeld, en vonden gemiddeld op 669 m van het nest plaats. Naarmate het broedseizoen vorderde, steeg het aantal vangsten per dag. Het gemiddelde prooigewicht was 232 g. Een kleine 50% van de prooien werd in bebouwd gebied bemachtigd, vooral in achtertuintjes. De mannetjes jaagden het meest vanaf een zitpost (49%), gevolgd door schroeven en stootduiken (33%) en contourjacht (11%). Daarbij werden forse individuele verschillen opgemerkt. Zo gebruikte één mannetje een hoge zitpost om als een Slechtvalk *Falco peregrinus* op een prooi te kunnen duiken. Twee andere hopten laag over daken, auto's en hekken om Stadsduiven *Columba livia*, Eksters *Pica pica* en Merels *Turdus merula* in tuintjes te verrassen. Eén mannetje gebruikte de avondschemering om bij kunstlicht, en onder gebruikmaking van zitposten als daken, schoorstenen en balkons (iets wat hij overdag nooit deed), slapende Stadsduiven te overrompelen.

In vergelijking met Haviken in rurale gebieden buiten Hamburg hadden de stadshaviken een klein activiteitsgebied, waarschijnlijk omdat de jachtmogelijkheden in de stad beter zijn (dat laatste bleek in ieder geval uit de geringere vliegactiviteiten en het hogere jachtsucces). Is daarmee de stad een gunstiger leefomgeving voor Haviken dan bos of platteland? De hogere broeddichtheid en dito jongenproductie in Hamburg, Keulen en Berlijn lijken daar wel op te wijzen, evenals de geringere sterfte onder adulte en juveniele Haviken (in Hamburg). Blijft de vraag: waarom werden steden niet eerder gekoloniseerd als ze kennelijk zo'n gunstige leefomgeving vertegenwoordigen? (RGB)

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